BRACHIOPODS FROM CARBONATE SANDS OF THE AUSTRALIAN SHELF

By J. R. RICHARDSON

Museum of Victoria, 285 Russell Street, Melbourne, Vic. 3000.

ABSTRACT: Three new genera, *Anakinetica* and *Parakinetica* (Terebratulida, Terebratellidae, Magadinea) and *Aulites* (Rhynchonellida, Cryptoporidae), and 2 new species, *Parakinetica stewarti* and *Magadinella mineuri,* are described. All 5 species are found in biogenic sands of the Australian shelf and differ in their adaptations for life in these sediments. Magadinid species use the pedicle to move individuals so that a stable position at the sediment/water interface is maintained. The rhynchonellid is a sedentary form fixed by the pedicle to the undersurfaces of free-living bryozoan species. Magadinid species are the dominant brachiopods in Australian shelf sediments in noteworthy contrast to their absence in New Zealand and Antarctic shelf faunas.

Living brachiopods in southern seas are not confined to rocky coastlines and reefs. In the Antarctic and Subantarctic (Foster 1974) and in New Zealand (Richardson 1981a) they are the dominant or co-dominant macroinvertebrates in a variety of depositional environments. Species within the Subfamily Terebratellinae are the commonest forms in Antarctic and New Zealand waters. All occupy soft substrates, some exclusively (*Gyrothyris, Neothyris*), while others (*Magasella, Waltonia*) are opportunistic and may live as either cliff hangers or bottom dwellers (Richardson 1981b).

Brachiopods are also common on soft substrates of the Australian shelf and are of interest for the following reasons:

1. With one exception, they are members of a subfamily (Magadinae) unknown in modern seas in any other area;
2. The four magadinids and one rhynchonellid described are specific to the bryozoan sands that are continuous along southern Australia (Wass, Conolly & McIntyre 1970); and
3. They display a variety of adaptations of the pedicle which is related to the occupation of a soft substratum.

SOURCES OF MATERIAL

Living individuals of all species studied were collected from Bass Strait during a cruise on Tangaroa, a research vessel of the New Zealand Oceanographic Institute (now Division of Marine Research, Department of Scientific and Industrial Research). Samples from this cruise are held by the Division in Wellington (Q register) and by the Museum of Victoria, Melbourne. Locality data for these and other stations sampled in Bass Strait are listed by Wilson & Poore (in press) — registration numbers of Museum of Victoria material are prefixed NMVBSS. Dried and preserved material has also been studied from the collections of the Museums of Western Australia (WAM), South Australia (SAM), the Australian Museum (AM) and the British Museum of Natural History (BMNH).

The sediments from which all species were collected have been described in the publications of Wass, Conolly and McIntyre (1970), Marshall and Davies (1978), Jones and Davies (1983) and Quilty (1985).

SYSTEMATICS

Superfamily TEREBRATELLACEA King 1850
Family TEREBRATELLIDAE King 1850
Subfamily MAGADINAE Davidson 1886

DIAGNOSIS: Differentially thickened Terebratellidae with permesothyrid foramen; cardinalia consisting of socket ridges, crural bases, and a cardinal process with trefoil posterior surface; loop axial to teloform.

GENERA INCLUDED: *Anakinetica* n.gen.: Tertiary and Recent, Australia (*Terebratella Cumingii* Davidson 1852). *Australiarcula* Elliott 1959: Cretaceous, Australia (*Australiarcula artesiana* Elliott 1959). *Magadina* Thomson 1915: Tertiary, New Zealand (*Magadina browni* Thomson 1915). *Magadinella* Thomson 1915 Tertiary and Recent, Australia (*Magadinella Woodsiana* Tate 1880). *Magas* Sowerby 1816: Cretaceous Europe (*Magas pumilus* Sowerby 1816). *Parakinetica* n.gen.: Tertiary and Recent, Australia (*Parakinetica stewarti* n.sp.). *Pirothyris* Thomson 1927: Recent, Australia (*Magasella vercoi* Blochmann 1910). *Rhizothyris* Thomson 1915: Tertiary, New Zealand (*Bouchardia rhizoida* Hutton 1905). *Tanakura* Hatai 1936: Tertiary, Japan (*Tanakura tanakura* Hatai 1936).

Only those genera with species available for study have been placed under the heading "Genera Included". However, inclusion of the genera that Elliott and Hatai (1965) attributed to this subfamily in the Treatise is not disputed.

COMMENTS: The only living species (from four genera) described from this subfamily are benthic and confined to carbonate sands. The position of individuals at the surface of soft sediments is maintained by the pedicle system which is distinctive in character in each genus. Diagnostic features of genera are the areas used for attachment of the dorsal adjustor muscles and details of the beak — its length and curvature and whether deltidial plates are fused or discrete and the beak ridges sharp or

rounded. No living species from the same genus co-exist, but sufficient Tertiary species have been collected to show the characters that differentiate species. Three species included in *Anakinetica* (from Recent seas, Miocene & Oligocene deposits) differ in shell outline, in degree of convexity of the valves, and in the shape and relative size of the area occupied by the cardinal platform. The differences are slight but consistent and are easily identifiable. Other fossil species attributed to *Anakinetica* display an incurved beak and heavy posterior thickening, and secondary loss of the pedicle may be inferred from these characters.

Some of the genera (*Australiarcula, Rhizothyris, Tanakura*) described from fossil species are similar in character to *Anakinetica* and *Parakinetica*, i.e., with a solid cardinal platform without a hinge trough and with attachment areas of the dorsal adjustor muscles in the posterior position indicating ratchet-like movements of a free pedicle. *Australiarcula artesiana* was described from glauconitic sands of the Great Artesian Basin (Elliott 1959, Parkin 1969), *Tanakura tanakura* from coarse-grained sandstones in Japanese Miocene deposits, and numerous species of *Rhizothyris* occur in greensands and bryozoan calcarenites of the New Zealand Tertiary (Thomson 1915, Allan 1960, Bowen & Campbell 1973).

The non-terrigenous character of the sediments occupied by members of the subfamily is noteworthy. All living species have been collected from bryozoan sands while members of fossil genera have been described from chalks, calcarenites and greensands.

It is not possible to define any ancestor/descendant relationships in different genera because all are specialised for benthic life in a particular type of sediment. Comparison with the subfamily Bouchardiinae illustrates this point. The latter family contains four genera, three (*Neoobouchardia, Bouchardia, Bouchardiella*) specialised for life in biogenic sands, one (*Malleia*) with characters associated with a sedentary life style (Richardson 1973) and so it is possible to differentiate characters associated with life style from those that suggest common ancestry, e.g., the shape of the cardinal process and the absence of crural bases. The trefoil shape of the cardinal process of the Magadinae is probably a familial character but cannot be confirmed as such in the absence of genera that occupy different substrates and follow a different life style.

Genus **Anakinetica** gen. nov.

ETYMOLOGY: From the Greek *ana* (up) *kineticos* (moving).

TYPE SPECIES: *Terebratella (?) Cumingii* Davidson 1852.

DIAGNOSIS: Beak large, suberect to nearly straight; deltidial plates fused, wide, flat; cardinal margin straight or nearly straight. Cardinal platform with posterior pits for attachment of the dorsal adjustor muscles. Loop annular to trabecular.

GEOLOGIC OCCURRENCE: Eocene to Recent.

LOCALITY: Australia.

COMMENTS: The type species of *Magadina* is *M. browni* from Waipara, New Zealand. In this and other New Zealand species attributed to *Magadina,* components of the cardinalia are not fused together to form a solid platform, the cardinal process is not swollen, and a deep hinge trough separates the crural bases. Thomson noted the difference between the two groups of species — "Cardinal process in primitive species (genotype) small but confined to the umbonal end of the hinge-trough, in advanced species (*M. cumingi*) large and swollen completely filling the hinge trough" (1927, p. 275). Growth stages of *A. cumingi* described below indicate that the crural bases also contribute to filling the hinge trough — they fuse medially with each other and with the anterior surface of the cardinal process.

Anakinetica includes one living species and three Tertiary species formerly included in *Magadina—Terebratula compta* Sowerby 1845 (Oligocene-Miocene), *Terebratella tenisoni* Tenison-Woods 1865 (Oligocene-Miocene), and *Magasella deformis* Tate 1880 (Upper Eocene). In addition, collections made from Beaumaris, Victoria (U. Miocene) and from the Jandakot Bores in Western Australia (Pleistocene) show that members of the genus were a common component of Australian shelf faunas during the Tertiary. Characters that separate species are adult loop stage, configuration of the cardinal platform, and details of the beak.

Anakinetica cumingi (Davidson 1852)
Fig. 1

Terebratella (?) Cumingii: Davidson 1852a, p. 78, pl. 14, figs 10-16.
Terebratella (?) Cumingii: Davidson 1852b, p. 368.
Terebratula (Bouchardia) Cumingii: Reeve 1861a, pl. 8, fig. 30.
Terebratula (Bouchardia) Cumingii: Reeve 1861b, p. 179.
Terebratula (Bouchardia) fibula: Reeve 1861b, p. 180.
Magasella Cumingii: Dall 1870, p. 137.
Magasella (?) cumingi: Davidson 1880, p. 18.
Magasella Cumingi: Davidson 1886, pp. 97-99, pl. 17, figs 23-32.
Magasella cumingi: Verco & Blockmann 1910, p. 97.
Magadina cumingi: Thomson 1915, p. 400, fig. 12.
Magadina cumingi: Thomson 1927, pp. 275-277.
Magadina cumingi: Cooper 1973, p. 30, pl. 5, figs 39-42.
Magadina cumingi: Richardson & Watson 1975a, pp. 381-382, fig. 1.
Magadina cumingi: Richardson & Watson 1975b, pp. 379-387, figs 1-7.
Magadina cumingi: Richardson 1979, pp. 415-417, 424-428, 432, figs 2, 3, 12.
Magadina cumingi: Mineur & Richardson 1984, pp. 327-334, figs 1-2.

TYPE LOCALITY: Port Jackson Heads, N.S.W.

TYPES: Davidson Collection, British Museum (Natural History).

OCCURRENCE: Medium to coarse carbonate sands, Australian shelf, between latitudes 31° and 39°S, longitudes 113° to 154°E, depths of 22-155 m. Stations NMVBSS

53, 59, 80-1, 118, 120, 161-2, 164, 166, 171, 173, 179, 183, 185-6, 189, 192-3, 199-206, 220; SAM 4862; WAM 19-71, 74-71, 77-71, 88-72, 272-86, 273-86, 274-86, 291-86, 306-86, 317-86, 346-86.

COMMENTS: Davidson (1852a) described *Terebratella (?) Cumingii* from two specimens which were believed to have been collected in New Zealand waters. In the Challenger Reports (1880) Davidson recorded *Magasella (?) cumingi* from Port Jackson Heads, New South Wales, and in 1886 he confirmed its occurrence in Port Jackson and stated that when first described "only two dead specimens were known in this country (England) and their habitat was uncertain." (p. 98). Davidson (1886) also considered *Terebratula (Bouchardia) fibula* of Reeve, collected in Bass Strait, to be synonymous with *A. cumingi*. Reeve (1861) stated that *Terebratula (Bouchardia) fibula* differed from *A. cumingi* in possessing a flat deltidium whereas the deltidium of *A. cumingi* is excavately grooved. As Davidson (1886, p. 98) points out — "The area in *M. Cumingi* is, it is true, usually excavated or concave, but in some examples it is almost flat, and upon that slight apparent difference it would not be right, I think, to record it as a separate species."

Specimens collected in Bass Strait, Victoria were used for the photographs in Fig. 1. This material has been compared with Davidson's specimens (in the British Museum, Natural History), and other specimens collected in Port Jackson, N.S.W., and they are considered to be conspecific. The illustrations of the loop (pl. 17, figs. 30 and 31) in Davidson's paper of 1886 are inaccurate. The two curved lamellae (which fuse to form the ring) are depicted with their lines of attachment on the sides of the septum a short distance below its crest. In all specimens observed by the author, both the lamellae and the ring lie flush with the crest of the septum, a condition also illustrated by Davidson (1852, pl. 14, fig. 15) in his original description of the species. This difference in Davidson's two papers may be accounted for by the fact that Davidson himself was the lithographer of the illustrations in his paper of 1852, but not in the paper of 1886 that was published posthumously.

The lophophore, pedicle, muscles and other soft structures and their relationship to hard parts are described in detail in Richardson and Watson (1975b) and Mineur and Richardson (1984). The distinctive cardinal platform of adults of *A. cumingi* (Fig. 1G, J) is derived from the fusion of socket ridges, crural bases, and the posterior surface of the cardinal process and stages in this process are described below.

GROWTH SEQUENCE: At 3 mm dorsal valve length the various components of the cardinalia can be distinguished on the thickened posterior region of the valve (Fig. 1H). The socket ridges converge posteriorly to fuse with the lateral borders of a bowl-shaped cardinal process. The crura are visible and their swollen bases are distinguishable from the socket ridges by shallow grooves. Medially, a deep hinge trough extends for almost the full length of the cardinal platform. A high median septum bearing two curved lamellae is restricted to the mid-region of the valve.

At 3.5 mm dorsal valve length, the posterior limits of

the crural bases are fused medially and with the anterior (smooth) surface of the cardinal process. Two pits are thus cut off on either side of the cardinal process; they are bounded posteriorly by the median borders of the socket ridges and anteriorly by the posterior borders of the crural bases. Between the cardinal platform and the elevated median septum, the median region of the valve floor is thickened as a rounded elevation. Crural processes extend from the crura and rudiments of the descending branches from the septum.

At 4.5 mm dorsal valve length, the crural bases are fused medially, the median line of fusion being visible anteriorly but not posteriorly. The shallow grooves which marked the lines of fusion of the socket ridges and crural bases are no longer visible but a new pair of grooves is evident on the surface of the now solid cardinal platform. These grooves run from the anterior borders of the pits flanking the cardinal process and converge slightly anteriorly. The descending branches are complete, and the lamellae extending from the crest of the septum are discrete.

The adult form results from further fusion and thickening of the cardinalia so that the anterior border of the platform is straight and not indented. The median septum has merged indistinguishably with the median thickening of the valve floor, and has grown in an anterior and ventral direction so that the lamellae lie not on the septal crest but on its posteriorly facing slope. The adult loop of *A. cumingi* is characteristically annular but in old specimens the lines of attachment of the descending branches may coalesce giving the haptoid type of loop.

Genus **Parakinetica** gen. nov.

ETYMOLOGY: From the Greek *para* (sideways) *kineticos* (moving).

TYPE SPECIES: *Parakinetica stewarti*, new species.

DIAGNOSIS: Beak small, straight; deltidial plates disjunct. Cardinal platform with posterior pits for the attachment of dorsal adjustor muscles. Loop annular.

GEOLOGIC OCCURRENCE: Recent.

LOCALITY: Australia.

COMMENTS: The characters separating *Parakinetica* from other members of the subfamily are beak form and shell shape. The beak is short with disjunct deltidial plates and the shell is plano-convex. Deltidial plates are fused in all other genera attributed to this subfamily.

Similarities in the cardinalia of *Anakinetica* and *Parakinetica* show that, in each genus, dorsal adjustor muscles are used to push the pedicle into the surrounding sediments. However, although the same movements enable individuals to surface in carbonate sands, differences in the grades of sands they occupy are evident from the processes of the pedicle; in *Anakinetica* they are short, stout and terminal, in *Parakinetica* relatively long and slender and scattered along the distal portion of the shaft. Differences in the disposition of the processes are evident in the fused deltidial plates of *Anakinetica* and the disjunct plates of *Parakinetica*.

A number of collections from Australian Janjukian (Late Oligocene) deposits include individuals with the diagnostic characters of this genus.

Parakinetica stewarti sp. nov.
Figs. 2, 3

The species is named after Mr. Ian Stewart in recognition of his assistance in numerous brachiopod projects.

DESCRIPTION: Pale grey to white. Maximum observed length 6.5 mm, breadth 6.0 mm, depth 3.0 mm. Dorsal outline broadly ovate; plano-convex, dorsal valve with pair of posterior ridges converging at the umbo, ventral valve carinate. Anterior commissure sulcate; lateral commissures sinuate; cardinal margin slightly curved, tapering to a median point. Beak straight, deltidial plates disjunct.

Dorsal valve interior with well-marked pallial sinuses and adductor muscle impressions; lateral transverse ridges separating posterior thickened area containing sockets and cardinal platform. Cardinalia with thick, posteriorly-convergent, socket ridges, fused medially with crural bases; crural bases occupying central area of platform, fused posteriorly with anterior surface of cardinal process, forming anterior borders of deep circular pits for attachment to dorsal adjustor muscles; cardinal process with posterior surface, striated, triple-faceted with lateral wings diverging from flat dorsal base. Median septum high anteriorly, almost touching ventral valve, gradually tapering posteriorly to terminate as low ridge at anterior border of cardinal platform. Loop annular.

Ventral valve slightly thickened posteriorly. Hinge teeth thick, with subquadrate outline overhanging grooves for socket ridges. Median ridge low, running from point just anterior of cardinal margin to anterior margin of valve. Muscle scars not impressed.

Pedicle inert, total length approximately half shell length, with slender processes extending from dorsal surface of posterior one third of length of shaft, proximal process occupying gap separating deltidial plates when pedicle retracted. Pedicle muscles as for *Anakinetica cumingi*.

TYPE LOCALITY: NMVBSS 81-HK1-121, latitude 39° 01.0'S, longitude 143° 15.4'E, 82 m, fine sand.

TYPES: Holotype NMVF52910; paratypes NMVF 52911-19

OCCURRENCE: Fine carbonate sands of western Bass Strait, between latitudes, 38°48' to 39°26'S, longitudes 143°06' to 143°49'E, depths 77 to 115 m. Stations— NMVBSS 48, 49, 55, 80, 119, 162, 184, 194.

Genus **Magadinella** Thomson, 1915

TYPE SPECIES: *Magasella Woodsiana* Tate 1880.

DIAGNOSIS: Beak erect to nearly straight; deltidial plates fused, wide; cardinal platform with posterior hinge trough bordered anteriorly by short, solid hinge plates. Loop haptoid to teloform.

GEOLOGIC OCCURRENCE: Tertiary and Recent.

LOCALITY: Australia.

COMMENTS: The genus *Magadinella* was erected by Thomson (1915) for *M. woodsiana* on the basis of differences in outline, cardinal margin, and stage of loop development from those species attributed by him to *Magadina*. The hinge trough, used for attachment of dorsal adjustor muscles, distinguishes *Magadinella* from *Anakinetica* and *Parakinetica*. Size, shape and folding differentiate *Magadinella* from *Pirothyris*, the only other Recent Australian genus with a hinge trough.

The type species was described from Janjukian-Batesfordian (L. Oligocene-Miocene) calcarenites, and other collections from similar deposits show that the genus is well represented in the Tertiary.

Magadinella mineuri sp. nov.
Fig. 4

The species is named after Mr. Rudi Mineur in recognition of his assistance in numerous brachiopod projects.

DESCRIPTION: Shell white to salmon-pink to red, rarely white with longitudinal red stripes. Maximum observed length 21 mm, width 15 mm, depth 10 mm. Outline narrowly ovate to ovate; biconvex, the ventral valve deeper and carinate. Anterior commissure sulcate; lateral commissures sinuate; cardinal margin strongly curved. Beak erect to nearly straight; deltidial plates fused; beak ridges rounded.

Dorsal valve interior with prominent adductor muscle impressions extending from cardinal platform to anterior tip of septum. Cardinalia with posteriorly-convergent socket ridges, not projecting beyond valve margin, their anterior segments fused medially with crural bases; hinge trough wide posteriorly in area bordered by socket ridges, narrow and shallow in anterior area bordered by crural bases; cardinal process variable in size. Median septum blade-like, slightly higher anteriorly than posteriorly. Loop trabecular.

Ventral valve interior thickened posteriorly; beak cavity filled except for tunnel leading to foramen. Hinge teeth long, extending full widths of margins of palintropes.

Fig. 1—*Anakinetica cumingi*: A-G, ventral interior, ventral, lateral, dorsal, posterior, anterior and dorsal interior views of the shell. H, dorsal interior of posterior region of juvenile shell before fusion of the crural bases with the anterior surface of the cardinal process (scanning electron micrograph). I, diagrammatic longitudinal section to show pedicle system and adductor and diductor muscles. J, outline diagram of cardinalia showing areas of muscle attachment of diductors (horizontal stipple) to the posterior surface of the cardinal process and of the dorsal adjustors (diagonal stipple) to areas flanking the anterior surface of the cardinal process. K, reconstruction of a living individual in medium bryozoan sands. Bar scale=1 mm
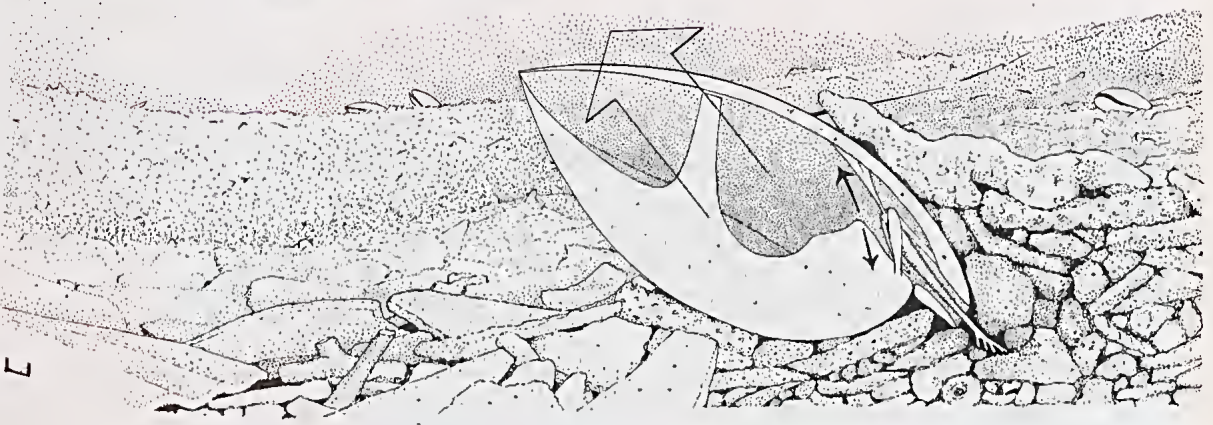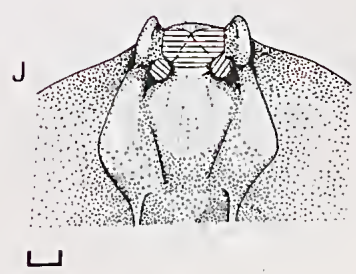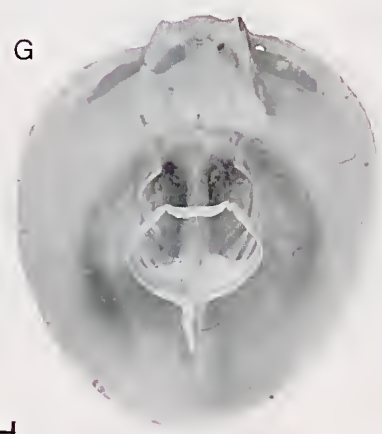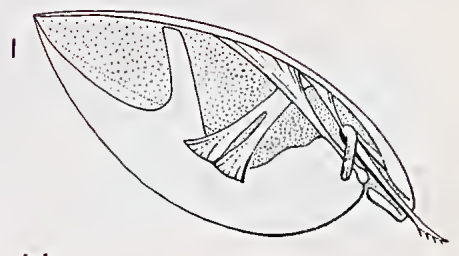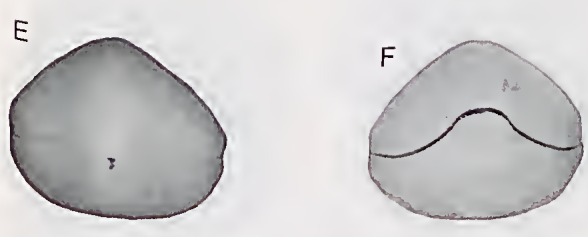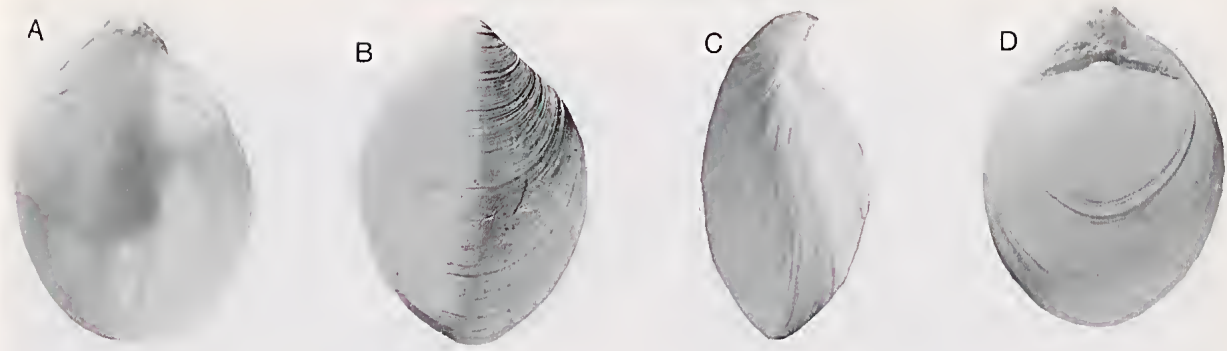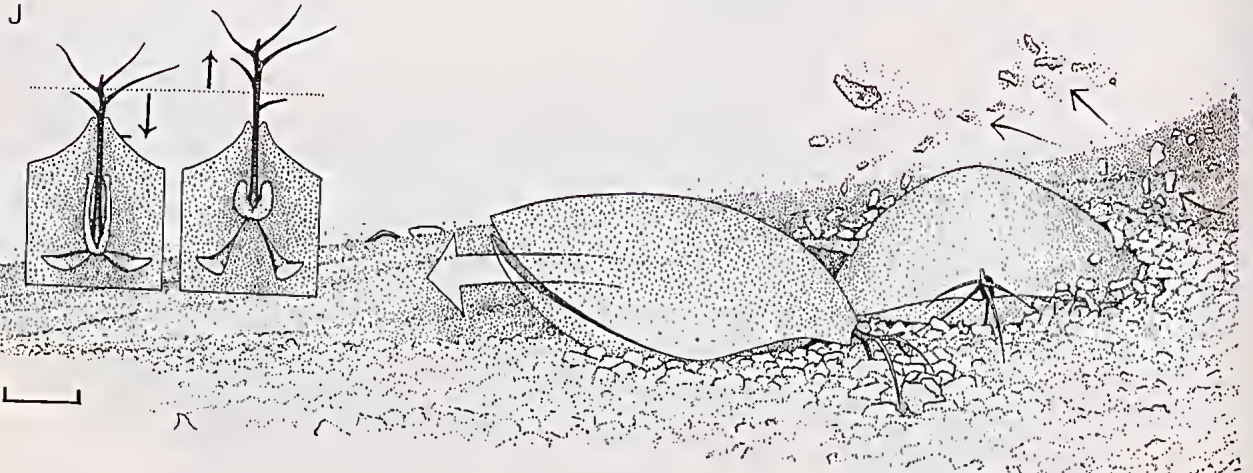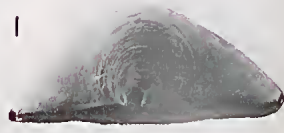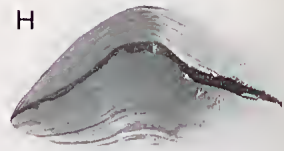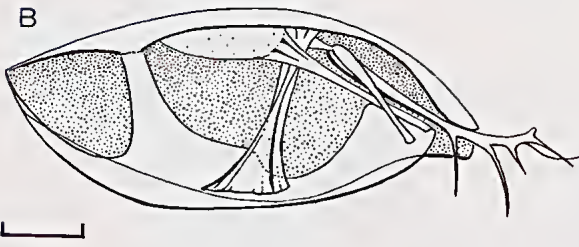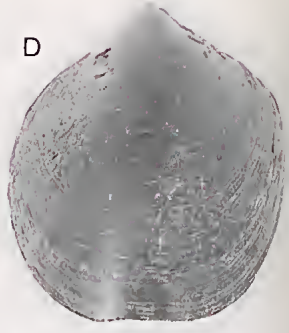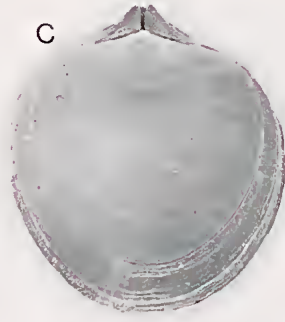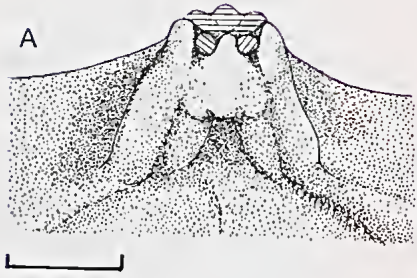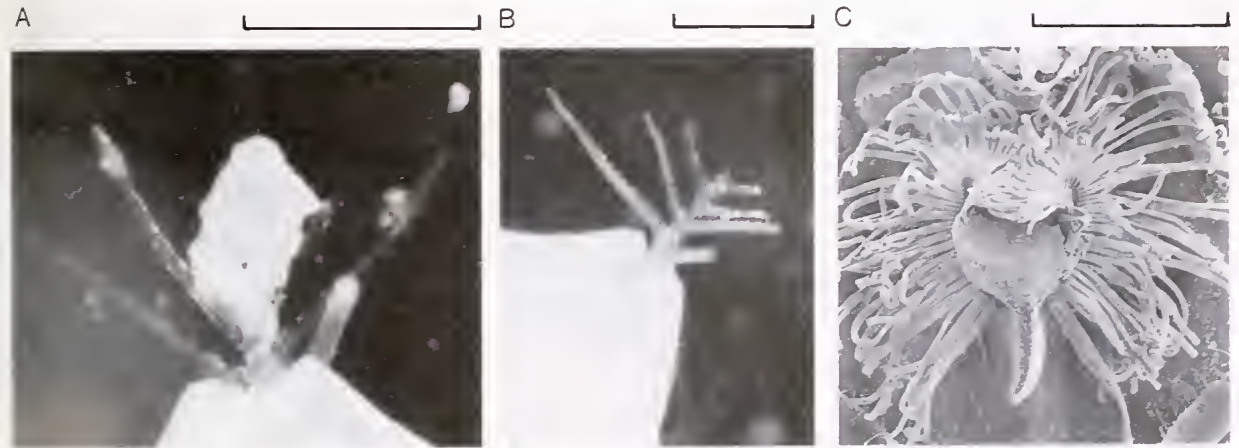
Fig. 3 — *Parakinetica stewarti*: Distal ends of pedicles of 2 individuals illustrating in A the grain of sediment used for larval bonding at the end of one process and B a later stage of development in which the processes are free of substrate. Growth lines are visible at regular intervals along the lengths of the processes.
C, scanning electron micrograph of the loop and lophophore.
Bar scale = 1 mm

Socket ridge articulating surfaces, shallow grooves underlying hinge teeth. Diductor muscle scars well-marked, extending anteriorly to at least half the length of valve.

TYPE LOCALITY: NMVBSS175, 39°06'S, 147°26'E, 63 m, sandy shell.

TYPES: Holotype NMVF52920; paratypes 52921-4.

OCCURRENCE: Bass Strait, Victoria (BSS 154, 173, 174, 175, 186, 199, 203, 204) between latitudes 38° to 40°S, longitudes 143°–148°E, depth 49 to 82 m.

Genus Pirothyris Thomson, 1927

TYPE SPECIES: *Magasella vercoi* Blochmann, 1910.

DIAGNOSIS: Uniplicate. Beak suberect; deltidial plates fused. Cardinal platform with a posterior hinge trough and solid anterior hinge plates. Loop haptoid.

GEOLOGIC OCCURRENCE: Recent.

LOCALITY: Australia.

COMMENTS: *Pirothyris* is the only terebratellid genus known with uniplicate folding and a shell in which depth is greater than width. In other genera, width is greater than depth so that a shell rests on the dorsal or ventral valve in contrast with shells of *P. vercoi* that lie on either side. Other living brachiopods with a similar depth/width relationship are members of the Terebratulacea. One example is *Liothyrella neozealanica* which is also uniplicate in folding. At present, this association of characters appears to be related to different orientations of the resting shell. Sedentary populations of *L. neozealanica* differ from the terebratellid and rhynchonellid species observed in the same area (Richardson 1981a) in that individuals are suspended by the pedicle. Thus they can occupy only the under-surfaces of rocks not their vertical or upper faces as do the terebratellids that lie on these surfaces.

Pirothyris differs from other living magadinids in that adults display a variety of substrate relationships as a result of variability in the length of the pedicle and the size of substrates used for settlement. Differences in pedicle length are not evident in hard structures.

In both *Magadinella* and *Pirothyris* the dorsal adjustor muscles are attached to a hinge trough which is bordered anteriorly by solid hinge plates. These two genera are also similar in the absence of well-defined palintropes and of beak ridges and in the strong convexity of the valves. However, the fact that depth is greater than width in *P. vercoi* means that the shell of this species rests on its side whereas that of *M. mineuri* rests on either valve.

Pirothyris vercoi Blochmann 1910
Fig. 5

*Magasella vercoi*: Blochmann 1910, pp. 91, 92, 98, pl. 27, figs 1-5.
Pirothyris vercoi: Thomson 1927, pp. 280-1, figs 94 a-c.
Pirothyris vercoi: Richardson 1975, pp. 197-205, pl. 15, figs 1-7.
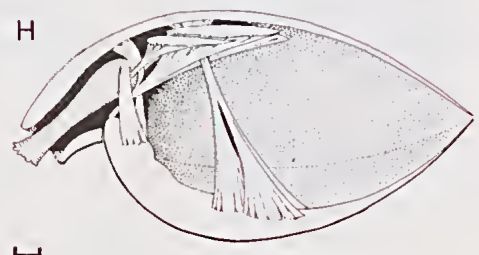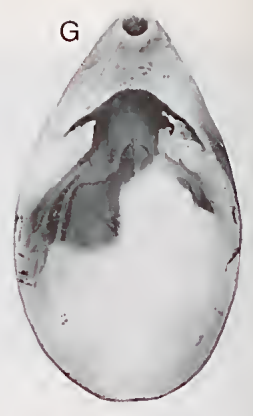
TYPE LOCALITY: Backstairs Passage, S.A.

TYPES: South Australian Museum, Adelaide, S.A.

Fig. 2 — *Parakinetica stewarti*: A, outline diagram of cardinalia showing areas of muscle attachment of the diductors (horizontal stipple) to the posterior surface of the cardinal process and of the dorsal adjustors (diagonal stipple) to areas flanking the anterior surface of the cardinal process. B, diagrammatic longitudinal section to show pedicle system and adductor and diductor muscles. C-1, dorsal, ventral, dorsal interior, ventral interior, lateral, anterior and posterior views of the shell (scanning electron micrographs). J, reconstruction of living individuals in fine bryozoan sands — inset diagrams showing pedicle movement.
Bar scale = 1 mm
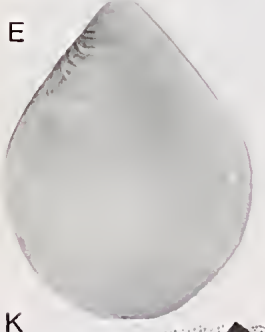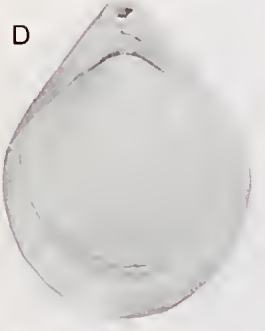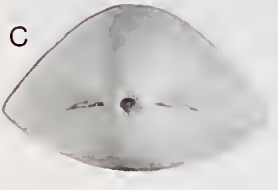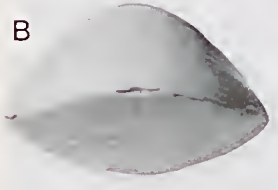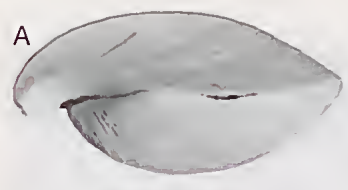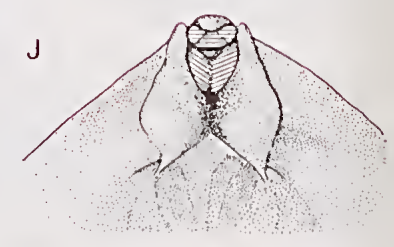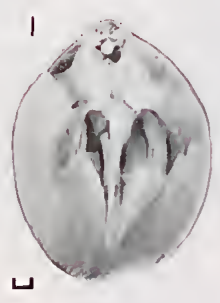
OCCURRENCE: Vereo's (1910) records give a number of localities in South Australian waters at depths of 22 to 300 m with the observation that the largest collections were made in Backstairs Passage at depths of 30 to 44 m. Collections identified by the author from Bass Strait (BSS 120, 183, 188, 192, 200, 203), and South Australia (Port Sinclair and Pearson Island), represent a range of latitudes 32° to 40°S, longitudes 133° to 144°E, depths of 48 to 85 m, on medium sand.

Superfamily RHYNCHONELLACEA Gray 1848
Family CRYPTOPORIDAE Muir-Wood 1955
Genus Aulites gen. nov.

ETYMOLOGY: *Aulites* Gk. m.=tent dweller.

TYPE SPECIES: *Atretia brazieri* Crane 1886.

DIAGNOSIS: Rectimarginate to uniplicate Cryptoporidae with outer hinge plates and without dental plates.

GEOLOGIC OCCURRENCE: Late Oligocene and Recent.

LOCALITY: Australia.

COMMENTS: With the transference of *Aulites brazieri* from *Cryptopora*, the Family Cryptoporidae now contains two genera. They differ from all other Recent rhynchonellids in beak characters (narrow, marginal deltidial plates bordering the delthyrium), erura (maniculifer), cardinal process (bilobate thickening), and in the median septum (high). Members of the family in which soft parts are known possess two pairs of adductor muscles and one pair of metanephridia, while one pair of adductors and two pairs of metanephridia characterise the members of other rhynchonellid families.

    Aulites brazieri is distinguished from species attributed to *Cryptopora* by the absence of dental plates and the presence of hinge plates. Other consistent differences are the larger foramen and narrower palintropes of the Australian species—external features associated internally with widely separated socket ridges and curved, not straight, erura. Since *Aulites* is a monotypic genus, the features that discriminate between species and genera are unknown. However, it is probable that the presence or absence of structures is more likely to separate genera than differences in the relative proportions of structures such as foramen and socket ridges which are likely species differentiators.

    Species of *Cryptopora* are found in most seas and at most depths—in abyssal as well as shallow waters. *Aulites brazieri* is the only living species found in Australia and is also the only species within the family in which distribution in relation to sediment is known. Living individuals are sedentary in habit and have been found only on the under-surfaces of species of free-living Bryozoa.

The species has been re-described because previous accounts do not include diagnostic characters or descriptions of soft parts.

Aulites brazieri (Crane, 1886)
Fig. 6

Atretia brazieri: Crane 1886, pp. 183-4.
Cryptopora brazieri: Hedley 1906, p. 467, pl. 36, figs 1-2.
Cryptopora brazieri: Cooper 1959, p. 18.

DESCRIPTION: Shell impunctate, white, smooth, delicate, translucent, with faint radial lines. Maximum observed length 2.9 mm, breadth 1.95 mm, depth 1.0 mm. Dorsal outline pyriform with pointed apex. Unequally biconvex, the ventral valve deeper, dorsal valve with two ridges converging at umbo. Anterior commissure rectimarginate; lateral commissures straight; cardinal margin slightly curved. Beak erect; deltidial plates discrete, narrow, marginal; foramen subapical, triangular; beak ridges sharp.

    Dorsal interior with socket ridges, short, widely separated. Outer hinge plates shelf-like, extending from dorsomedial borders of socket ridges, anteriorly continuous with crura. Paired thickenings, semi-circular in outline, occupying shell border between posterior extremities of socket ridges. Adductor muscle impressions wide, almost circular, area with anterior border just posterior to anterior limit of septum.

    Ventral interior with low median ridge in central region of valve. Pedicle collar incomplete, lining apex of valve interior, merging walls just posterior borders of hinge teeth. Muscle impressions not visible.

    Lophophore spirolophous. Intestine straight, without distal enlargement. Metanephridia one pair. Gonads reticulate.

    Adductor muscles two pairs, each with paired attachments to dorsal valve and single attachment to ventral valve; posterior adductors attached to area of dorsal valve between bases of socket ridges and posterior limit of septum, ventrally to mid-region of ventral valve in an area at the level of the hinge teeth; anterior adductors with broadly ovate attachments flanking median septum and terminating ventrally in mid-line of ventral valve anterior to posterior adductors. Diductor muscles paired, extending anteriorly to mid-region of valve; posteriorly the terminations of the paired muscles united by connective tissue with the muscular tissue attached to paired thickenings on the valve's posterior border and connective tissue to the area between the thickenings.

    Pedicle short with chitinous coat, attached to substrate close to foramen. Dorsal adjustor muscles thin, ribbonlike bands, running from lateral faces of the pedicle to junctions of the outer hinge plates and socket ridges; ventral adjustors extending from proximal end of pedicle

Fig. 4—*Magadinella mineuri*: A-E, lateral, anterior, posterior, dorsal, and ventral views of a shell. F, dorsal view of a shell with colour markings. G, ventral interior. H, diagrammatic longitudinal section to show pedicle system and adductor and diductor muscles. I, dorsal interior. J, outline diagram of cardinalia showing areas of muscle attachment of the diductors (horizontal stipple) to the posterior surface of the cardinal process (diagonal stipple) and of the dorsal adjustors (diagonal stipple) to the hinge trough underlying the anterior surface of the cardinal process. K, reconstruction of living individuals in coarse bryozoan sands.
Bar scale=1 mm

flanking adductor muscles, with attachments posterior to diductor muscles.

TYPE LOCALITY: Port Stephens, N.S.W., at 25 fathoms, sandy mud.

TYPES: Davidson Collection, BMNH.

OCCURRENCE: Janjukian (late Oligocene) Mallee Bore II, 430′ to 432′. Recent—NMVBSS 121, 194, both fine sand. WAM 290-86, 292-86, 293-86, 299-86, 301-86, 306-86. Queensland—Mast Head Island.

The shells of *Aulites brazieri* have been collected from depths of 34 to 228 m off the eastern, southern, and western Australian coasts, i.e. between latitudes of approximately 23° & 39°S and longitudes of 113° to 154°E. Collections from Bass Strait, Victoria, have shown that living individuals are found only on free-living bryozoans which are the dominant living organisms in sands collected from the Bass Strait stations listed above. Samples from these stations contain at least fifteen free-living bryozoan species (P. Bock, pers. comm.) and *A. brazieri* was found attached to *Selenaria maculata* and *Lunulites capulus*. The only other record of living specimens by Hedley (1906), also notes their presence on the undersurfaces of bryozoans but with no record of the sediment sampled.

COMMENTS: Cooper (1959) suggested that the Miocene species *Terebratella acutirostra* Chapman may be a synonym of *Aulites brazieri* and study of the holotype, the only specimen, confirms that, in external features at least, it is indistinguishable from *Aulites brazieri*.

FUNCTIONAL MORPHOLOGY

All the species described were collected live, but from depths (55-120 m) that prevented *in situ* studies. Consequently, the behaviour of individuals was observed in aquaria in the sediments in which they were collected. It is assumed that the movements of individuals would be similar in laboratory conditions to those in natural surroundings although their amplitude and frequency would probably differ.

Comparative anatomical studies of the four magadinid species showed that no differences are apparent in the form and disposition of nephridia, gonads, gut, digestive diverticula, or of the circulatory system as described in detail for one species, *Anakinetica cumingi*, by Richardson & Watson (1975b). The lophophore is plectolophous in all and differences in the extent of coiling of the spiral arm can be related to size, relative to total shell space, of the mantle cavity (Richardson & Watson 1975b). Adductor and diductor muscles are inserted on the same surfaces and occupy the same position relative to other structures.

PEDICLES: Of the soft parts, only the pedicle system differs in each of the four species, in the form of the pedicle and in the position of the muscles. In all species it is defined as "inert" (Richardson 1979), i.e., composed of a thick chitinous coat enclosing a fibrous core. Adults of two of the species (*Pirothyris vercoi* and *Magadinella mineuri*) studied retain the substrate used for larval settlement. In two others (*Anakinetica cumingi* and *Parakinetica stewarti*) it is outgrown at an early stage of development, and the pedicle is free with chitinous processes fringing its distal end. Either three (in *P. vercoi* and *M. mineuri*) or four (in *A. cumingi* and *P. stewarti*) pairs of pedicle muscles connect the head of the pedicle with the shell. The position of the ventral adjustors is similar in all species, and their contractions pull the pedicle into the shell. The action of the dorsal adjustor muscles differs according to the areas of the cardinalia used for their attachment. A posterior position, in pits flanking the cardinal process as in *A. cumingi*, means that these muscles are more or less parallel to the pedicle and so contractions will extrude the pedicle. In these species the median pedicle muscles are long, thin, and contractile and their contractions assist in the extrusion of the pedicle. Contractions of dorsal adjustor muscles that are attached to regions of the cardinalia anterior to the cardinal process (the hinge trough or plates) result in rotation of the pedicle. With adjustors in this position, the median pedicle muscles are short and fibrous and they hold the pedicle in position during contraction of the dorsal adjustors.

MOVEMENT: *Parakinetica stewarti* moves in similar fashion to *Anakinetica cumingi* by the ratchet-like action of a free pedicle (Figs 1, 2). However, although the muscles, their position, and their actions are similar in each species the direction of movement of individuals differs in each because they also differ in shell shape. *P. stewarti* is subcircular in outline with a flat dorsal valve and a short beak and contractions of the muscles result in movements that are roughly parallel with the surface of the sediment. The same movements in *A. cumingi*, which is biconvex and ovate, result in movement of the shell in an upward and forward direction. In *P. stewarti*, the pedicle processes are long and slender and extend from the lateral and dorsal surfaces of the distal portion of the pedicle. Differences in the length and position of the processes in these two species are linked with activity in sediments of different grain size. The short, thick, closely-spaced processes of *A. cumingi* are associated with movement in medium to coarse bryozoan sands, the long, thin processes of *P. stewarti* with that in fine sands.

Collections of young individuals of *Parakinetica stewarti* show that larvae settle on fragments that comprise the sands occupied by adults. The pedicles of in-

Fig. 5—*Pirothyris vercoi*: A-F, ventral, dorsal, ventral interior, posterior, lateral, anterior views of shells. G, scanning electron micrograph of dorsal interior. H-J, 3 individuals with pedicles of different lengths, each bonded with fragments of bryozoan colonies. K, outline diagram of cardinalia showing area of muscle attachment of the diductors (horizontal stipple) to the posterior surface of the cardinal process and of the dorsal adjustors (diagonal stipple) to the hinge trough underlying the anterior surface of the cardinal process. L, diagrammatic longitudinal section to show pedicle system and adductor and diductor muscles. M, reconstruction of living individuals in medium bryozoan sands. Bar scale=1 mm
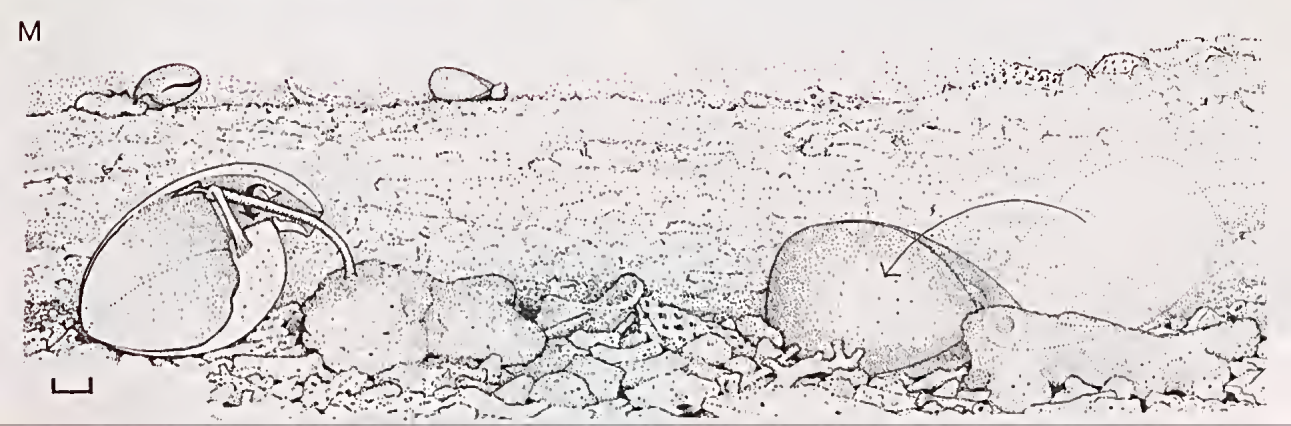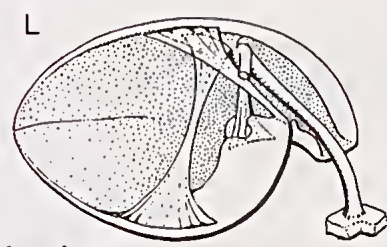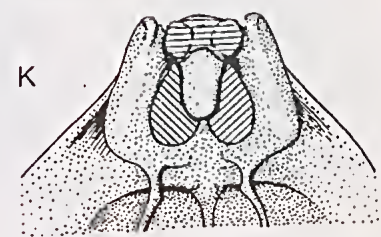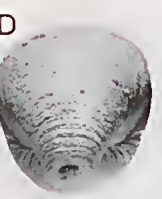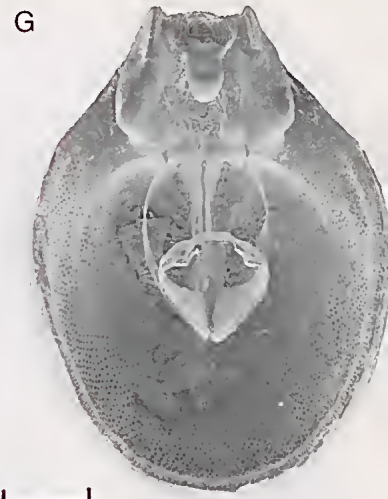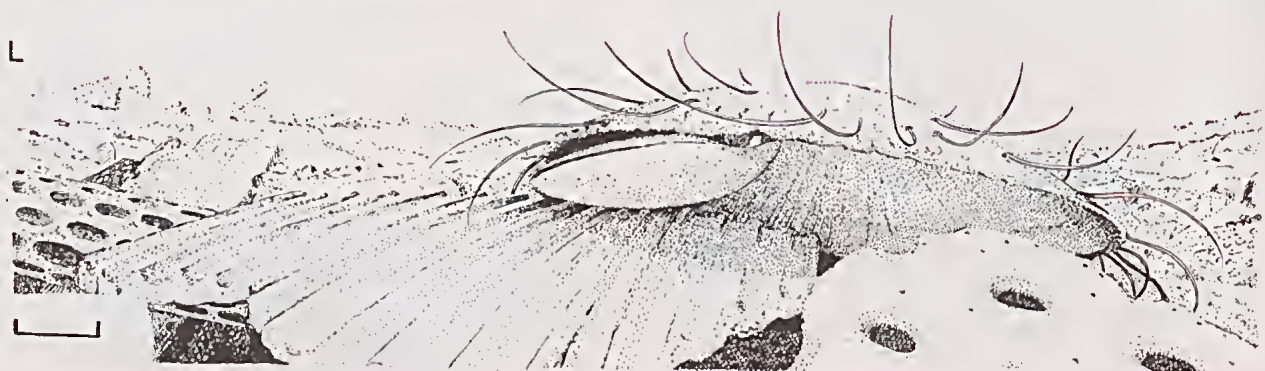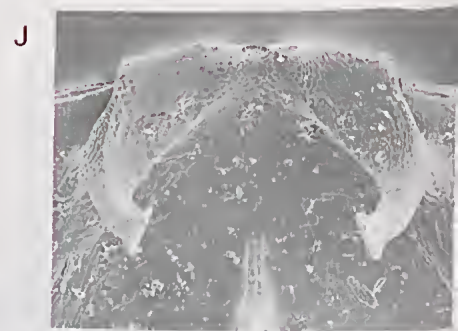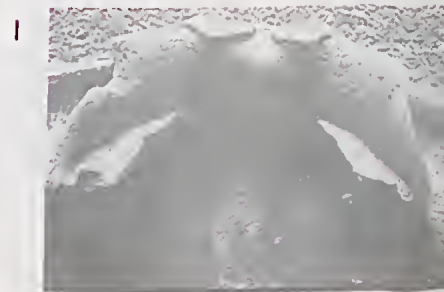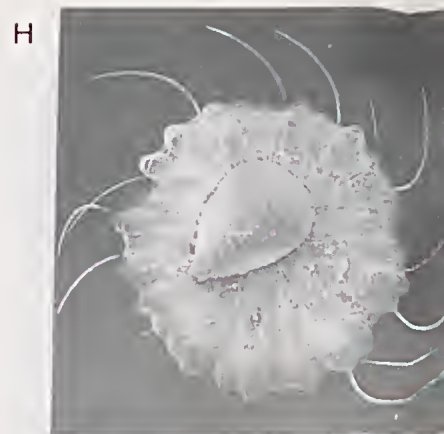
dividuals with a shell length of 1.5 mm display only two or three processes (Fig. 3A) with a fragment bonded to the tip of the pedicle's central shaft. That is, the tip of the pedicle retains the fragment used for larval settlement. Fragments have not been observed on the pedicles of most individuals larger than 1.5 mm. However, in those instances in which the fragment is retained, it is not fixed to the pedicle tip but appears as a ring around its shaft. The pedicle tip has apparently grown through and beyond the original site of bonding and disintegration and loss of the fragment occurs with growth. It is presumed that, as soon as the pedicle muscles operate as observed in adults, the larval substrate is not needed and could be an encumbrance to movements of the pedicle. It is emphasised that the bonded substrate is not lost by accident but by active growth, i.e., by progressive chitinisation visible as growth rings on the shaft and its processes (Fig. 3b).

Magadinella mineuri appears to be confined to coarse bryozoan sands in which larger fragments may approximate the mass of adult organisms (Fig. 4). The substrate is fixed permanently to the tip of the pedicle which is invariably short. Three pairs of muscles extend from the head of the pedicle—ventral and dorsal adjustors and ventral median pedicle muscles. The dorsal adjustors are attached to the floor of the hinge trough.

The living individuals displayed little movement when placed on the surface of sediments in aquaria. However, if they were covered with loose sediment, movements of either or both the shell and the pedicle with its bonded substrate would work the organism to the surface. Sediment on the shell results in contractions of the pedicle muscles, which connect the shell with the pedicle and its substrate, and contractions of these muscles will twist the lighter of the two bodies (shell or substrate). In an inert medium (sediment) alternate or successive movements of either shell or substrate give the organism a surfacing action. The capacity to twist appears to be an important attribute in this species with its short pedicle and consistently close connection with bonded substrates. As a consequence, the dorsal adjustor muscles are strong but the size of all muscles indicates a high level of activity. The median pedicle muscles in sedentary or opportunistic species consist of fibrous, non-contractile tissue whereas pink, contractile tissue is a major component in *M. mineuri*.

Pirothyris vercoi occupies medium to coarse bryozoan sands and individuals are bonded throughout life with fragments of varied mass and shape (Fig. 5). The processes that bond the pedicle to carbonate surfaces are not visible to the naked eye. The flexible pedicle also varies in length, it may be very short or approximately half the total length of the shell. Variation in both pedicle length and the mass of bonded substrate results in differences

in the movements of individuals. Three pairs of muscles extend from the head of the pedicle—ventral adjustors and median pedicles to the ventral valve, dorsal adjustors to the hinge trough in the dorsal valve. Contractions of the dorsal adjustor muscles together with the shell shape characteristic of this species (depth greater than width) result in rolling movements irrespective of pedicle length. A short stalk combined with substrate of mass equal to or less than the organism results in alternate or sequential movements of the shell and stalk that are also characteristic of *Magadinella mineuri*. Individuals with long pedicles have been observed to be bonded only with relatively large masses. In these individuals contractions of the dorsal adjustor muscles cause the shell to roll from side to side in response to sediment or water movements.

CHARACTERS ASSOCIATED WITH HABITAT AND LIFE STYLE: The movements that characterise the magadinid species result from differences in the position of the dorsal adjustor muscles, in the form of the pedicle and its processes, and in shell shape. Differences in muscle position and pedicle type are clearly reflected in the cardinalia and beak. The position of the dorsal adjustor muscles determines types of movement—attachment to pits in the posterior region of the platform shows that contractions extrude the pedicle, while insertions to the floor of the hinge trough indicate twisting movements. The position of the shell in relation to the sediment is evident from the beak ridges—sharp ridges show that the posterior end of the shell is the leading edge in movements within the sediment, while rotating or rolling movements are characteristic of species with rounded beak ridges. Deltidial plates are fused in species in which pedicle processes are restricted to the tip of the pedicle (whether free or bonded), deltidial plates are discrete in those in which processes are distributed along the shaft.

Other characters that may be associated with habitat and life style are size and the absence of ornament or epibionts. Occupation of shifting sediments (Richardson & Watson 1975a) requires continual adjustment so that individuals occupy a stable position to feed at the sediment/water interface. The mobility of these forms apparently inhibits the growth of epibionts that are so common on the shells of members of sedentary populations (Doherty 1979). Members of sedentary populations also form the principal settling surfaces for larvae (Wisely 1969). However, no member of any magadinid species has been collected with any brachiopod attached to the shell. The pedicles of the smallest shells collected are invariably bonded with grains of sediment. The larvae may thus exhibit preferential settlement, or they may settle at random but fail to survive on surfaces other than the roughened grains that predominate in the sediments they occupy.

Fig. 6—*Aulites brazieri*: A-G, scanning electron micrographs of dorsal, ventral, ventral interior, dorsal interior, posterior, anterior, lateral views. H, small individual fixed to the undersurface of the free living bryozoan colony, *Selenaria maculata*. I, cardinalia showing areas for the attachment of diductors on the posterior margin and hinge plates for the attachment of dorsal adjustor muscles. J, cardinalia showing complete maniculifer crura. K, diagrammatic longitudinal section showing adductors (2 pairs), diductors and pedicle system. L, reconstruction of individual fixed to the undersurface of living *Selenaria maculata*. Bar scale = 1 mm.

Various modifications of the pedicle and its muscles have been described which give magadinids the capacity to maintain a position at or near the sediment surface. In contrast, the surface position of the sedentary rhynchonellid, *Aulites brazieri,* is maintained by using free-living bryozoans as sites of attachment.

ACKNOWLEDGEMENTS

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